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Water relations in the soil crust lichen *Psora decipiens* are optimized via anatomical variability

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Abstract

Biological soil crusts are communities composed of cryptogamic organisms such as lichens, mosses, cyanobacteria and green algae that form a skin on soils in areas where vascular plants are excluded or limited by water availability or temperature. The lichen *Psora decipiens* (Hedw.) Hoffm. is a characteristic key organism in these communities in many different biomes. The species has a generalistic ecology and high morphological variation, which contributes to the ability of the species to withstand environmental changes. We investigated whether different populations, based on site and associated morpho-anatomical differences, incorporate functional water relations and how/whether this was mediated by changes in abiotic factors. Samples were collected from two climatically distinct sites, one "dry" site in southern Spain, and one "wet" site in the Austrian Alps. Our results showed that samples from the dry site had a significantly thicker epinecral layer, higher specific thallus area, a faster water uptake and contained more water per dry weight, all of which contributed to a much slower drying rate. Both populations showed a highly adjusted water gain that incorporates functional water relations and diffusion properties as a result of local water availability. We show eco-physiological and morphological mechanisms that underlie the high variability in *P. decipiens* and draw conclusions around the ecological benefits for this generalistic lichen species such as optimized water relations and light exploitation.

Keywords

Biological soil crusts, hydrological characteristics, epinecral layer, lichens, phenotypic plasticity, drying rate

Introduction

The concept of ecotypes, defined as distinct genotypes (or populations) within a species, resulting from adaptation to local environmental conditions (Hufford & Mazer 2003), describes the geographic variation within a species and the balance between local adaptation and intra-specific hybridization (Begon et al. 2006). In lichenology, to distinguish between differentially exposed populations, the concept of ecotypes can be used, for example to describe different altitudinal distributions (Nadyeina et al. 2014). Another interpretation of structural changes in lichen thalli from different populations is often described as phenotypic plasticity. For example, different rates of photosynthesis occur as a result of differences in thallus hydration, due to structural changes, when comparisons are made between north- and south facing populations of *Ramalina capitata* (Ach.) Nyl. (Pintado *et al.* 1997) and vagrant compared with attached thalli of *Cetraria aculeata* (Schreber) Fr. (Pérez-Ortega *et al.* 2012). Increasing the amount of rhizinae is a modification that can improve thallus hydration and therefore photosynthesis, when comparing epilithic versus epiphytic populations of *Parmelia pastillifera* (Harm.) Hale (Tretiach & Brown 1995). Finally, *Catillaria corymbosa* (Hue) I. M. Lamb, an Antarctic endemic species, showed an increased water retention capacity and therefore more photosynthesis in shaded localities (Sojo *et al.* 1997).

In drylands, vascular plants are limited due to low water availability and therefore biological soil crusts (BSC) become a dominant component of vegetation (Pointing & Belnap 2012; Büdel *et al.* 2014). BSCs also occur in high alpine areas above the tree-line, typically when the mean temperature of the warmest month is below 10°C (Körner, 1998), seventy to eighty percent of the precipitation falls as snow, and snow cover lasts 270 to 300 d (Auer et al., 2002). BSCs are small scale poikilohydric lichen-bryophyte and microbial communities that are considered to be ecosystem engineers (Pointing & Belnap, 2012) that stabilize soil (Belnap *et al*. 2003), and make significant contributions to the carbon and nitrogen fixation budgets (Elbert *et al.* 2012). Lichens often form the major proportion at the climax stage of these communities (Büdel *et al*. 2009). Studies on soil lichen populations, including their functional aspects and morphological differences, are need to enable us to

predict climate change scenarios in these areas; these habitats are considered to be at high risk in recent climate change projections (IPCC 2012).

Here we studied the differences in morpho- anatomical and hydrological traits of two populations of *Psora decipiens* (Hedw.) Hoffm., a typical lichen occurring in the climax stage of biological soil crusts worldwide (Büdel 2003, Galun & Garty 2003, Rosentreter & Belnap 2003. Two contrasting areas with distinct populations were selected: a high alpine environment ("Site Hochtor", Fig. 1A) and arid badlands ("Site Almeria", Fig. 1B). Preliminary observations indicated (1) strong variance in overall thallus structure and appearance and (2) higher vitality of the alpine population (based on mean thallus size and vivid color). Based on this field observation we hypothesized, that local water availability is a major driver for morpho-anatomical differences in lichens and thallus water relations can be optimized to local necessities.

Material and Methods

Study sites, organisms and sampling

We chose two sampling sites that support natural BSC occurrence, but differ considerably in their environmental conditions. The first, and humid "Site Hochtor", was a high alpine area at an elevation of 2500 to 2600 m asl. of the Großglockner massif, Austria. The second site was the dry site, "Site Almeria", located in South East Spain. This location was considered as one of the driest and sunniest in Europe, and has been described in previous studies (Lázaro *et al.* 2001, Cantón *et al*. 2004).

Psora decipiens is a pale pink squamulose-crustose lichen with conspicuous white-pruinose, often upturned margins. The lower cortex is white, poorly developed or absent and the attached hyphal net penetrates into the substrate. It is a cosmopolitan lichen and is well known as indicator species for intact BSC climax stages (Fig. 1C and D).

Samples (30) were randomly collected at each site in areas with homogenous BSC cover and no shading from plants. Each sample unit was a 9.2 cm² section of an intact *P. decipiens* dominated BSC, where several thalli were growing. Sampling at site Hochtor took place in August 2013 and at site Almeria in June 2013. Samples were dried at room temperature within 3 d of collection, transported

and stored frozen. In the laboratory the surrounding soil crust was removed from the thalli, which were then washed. The number of replicates used in each experiment is indicated below.

Climate measurements

Both investigation sites were equipped with similar climate stations, capable of monitoring air temperature and humidity, solar radiation (Photosynthetically Active Radiation, PAR), $UV_{(A+B)}$-radiation and precipitation. Climate data were recorded from both sites over 2 y, from April 2012 - March 2014 at site Almeria, and from August 2012 - July 2014 at site Hochtor. Air temperature and relative humidity were measured 1.5 m above ground, and solar radiation at 2 m above ground. The snow cover was estimated from the length of time the various sensors were inactive. Mean (± standard deviation) values were calculated for summer and winter air temperature, humidity, PAR and UV_A and UV_B combined radiation. Additionally maximum and minimum temperature, and maximum UV and PAR radiation were extracted from the dataset.

Thallus morphology and anatomy

Thickness. The thicknesses of the lichen thalli, the epinecral layer, the photobiont layer and the medulla were measured on freezing microtome sections, n= 400 for the photobiont layer and medulla measurements and n= 100 for the epinecral layer measurements from each site, using the AxioVision software (Carl Zeiss, Jena, Germany). To visualize thallus internal relationships between photo- and mycobiont, the ratio between the photobiont layer and medulla was calculated.

Specific thallus area. To calculate the specific thallus area (STA, $mm^2\ mg^{-1}$) thallus size was first determined by binocular microscopy using the above mentioned software. A standard procedure was used to delineate the extent of each lichen thallus. The lichen thalli were wetted to ensure maximum surface area, placed on scale paper and photographed. The corresponding dry masses (DM) of these thalli were determined by weighing after 3 d of oven drying at 60°C (n=20).

Specific thallus mass. This parameter was emphasized by Kershaw (1985) as an important lichen parameter for water loss and water uptake and is the inverse equivalent of STA (see above).

Hydrological traits

Drying rate. Photosynthetic activity was monitored by measuring the efficiency of PSII photochemistry using an imaging-PAM chlorophyll fluorometer (Heinz Walz, GmbH, Effeltrich, Germany). Specimens of roughly the same size (± 10 mm²), which had been submerged in water overnight, were first weighed, then placed in a sealed plastic chamber on a wire net over a saturated NaCl solution which maintained a level of humidity of 75% rH equivalent to a water potential of -37 MPa at room temperature (Pardow & Lakatos 2013). Initially the maximum quantum yield of PSII F_v/F_m of the hydrated and dark adapted (30 min) samples was measured as a reference. Subsequently, short saturation pulses were applied every 2 minutes to determine the fluorescence parameters for calculating PSII yield (Y= Fv/Fm). The time was measured until a threshold of 0.2 PSII yield was reached for n=18 replicates (3 thalli per chamber). To determine the absolute water loss during the measurement, samples were weighed again, directly after the measurement. Drying rate was calculated, and expressed as the time need for 1 µl of water to evaporate from one mm² of thallus (min μl^{-1} mm^{-1}).

Water uptake. To ensure full water saturation prior to weighing, the samples were submerged in distilled water for 30 min. Excessive water and droplets were carefully shaken off before measurement of maximum wet mass (WM_{max}). The corresponding dry mass (DM) of these thalli was determined by weighing after 3 d at 60°C. The maximum water uptake relative to the thallus specific dry mass of the samples (n=36) was calculated as WM_{max} – DM/ DM (Pérez 1997).

Repellency. To measure water repellency/hydrophobicity of individual lichen thalli, the water drop penetration time (WDPT) was measured for n= 30 replicates. The WDPT test consists of placing a drop of water on the surface of the epinecral layer and measuring the time until complete absorption occurs. This is a commonly used test because of its simplicity (Letey *et al.* 2000) and the value of information it provides, as it was considered to be the most indicative and sensitive way for the hydrological consequences of water repellency to be investigated (Doerr 1998, Leelamanie *et al.* 2008).

Optimum water content. CO_2 gas exchange measurements were conducted under controlled laboratory conditions using a portable mini cuvette system (GFS 3000, Walz Company, Effeltrich, Germany). The response of net photosynthesis (NP) and dark respiration (DR) to thallus water content (WC) was determined for three replicates (each replicate was composed of about 20 individual squamules) from each of the sites. Complete drying-out cycles (from water saturated to air dry thalli) were measured at 750 µmol photons m^{-2} s^{-1} (saturating light), ambient CO_2, at 17°C (which is within the optimal temperature range for CO_2-gas exchange of this species). Samples were weighed between each measurement and thallus water content (WC) was later calculated as a percentage of dry mass. Dry mass was determined after five days in a desiccator over silica gel. Ninety percent of maximum net photosynthesis was considered to be a reasonable estimate for optimal water content.

Water holding capacity. Water-holding capacity (WHC) was calculated by: saturated wet mass – dry mass (mg) / thallus area (cm^{-2}) after shaking surplus water off the lichen thallus. The corresponding dry mass (DM) of these thalli (n=20) were determined by weighing after drying for 3 d at 60°C. Thallus area was measured as described above.

Statistics

To determine differences between the lichens anatomical features and the climate of the two sites student's t-tests were used (Statistica 10, Stat soft). All data was normally distributed. Significance level was defined at $P < 0.05$.

Results

Climate measurements

The data (Table 1) demonstrate the pronounced differences in temperature, humidity and precipitation between the sites, and also within the sites based on seasonality. In Almeria it was significantly warmer, drier and brighter than at the alpine site Hochtor. However in site Hochtor the growing season only lasted about 3 months in a year, due to the persistent snow cover.

Thallus morphology and anatomy

Thalli from Almeria had thicker epinecral layers, but only half the medulla thickness compared to samples from Hochtor (Fig. 1E and F; Table 2). The photobiont layer showed no difference between the sites, therefore, the photobiont layer to the medulla-ratio of the thalli from site Almeria was twice as high. This indicates significant differences in the internal structure of the thalli between the populations. STA was also higher for samples from site Almeria (Table 2), indicating that these thalli can support relatively large areas despite their reduced thallus matter. Corresponding to this finding, STM was significantly higher for samples from site Hochtor, indicating that these samples are thicker than those from site Almeria.

Hydrological traits

Both populations had similar water holding capacities per area (Table 2) and showed some common drying characteristics, independent of sampling site and thallus size (Fig. 2). For example, the initial activity of PS II was similar, with high yields of PSII at ca. 0.6 (blue color, Fig. 2). Additionally, these levels of activity remained relatively stable for certain amounts of time independent of thallus size (around 0.6). As soon as a threshold of desiccation was reached, the actual drying event occurred quickly, and no fluorescence signal could be detected shortly after this. In contrast to these common features, the actual drying rate was different between the two populations. Thalli from site Almeria dried six-times slower than those from site Hochtor (Table 3, Fig. 2). Additionally, *P. decipiens* specimens from site Almeria took up water faster (1.2 ± 0.27 sec compared to 168.4 ± 15.8 sec for samples from site Hochtor) and contained more water per dry mass than those from site Hochtor (Table 2). The optimum WC for CO_2 exchange extended over a significantly narrower range, (109-156 % DM) for samples from site Almeria than for samples from site Hochtor (131-195 % DM).

Discussion

In the present study we have demonstrated distinct differences between two populations of the lichen species *P. decipiens,* derived from climatically contrasting habitats. Morpho-anatomical differences appear to be reflected in differences in functional water relations and diffusion properties as a result of local water availability. We have identified eco-physiological and morphological mechanisms that underlie the high variability in *P. decipiens* that determine its ecological fitness in a particular habitat.

The most striking difference between the two populations is water gain. Considering the differing STA and the maximum water uptake relative to the thallus specific dry mass, thalli from both sites have the same water holding capacity on an area basis (WHC in Table 2). This indicates that, not only surface area, but also thallus internal structure must be studied to understanding the drying processes in lichens. During the actual drying process we need to consider the amount of water in the thallus, based on thallus area. The resulting calculation shows that drying from optimal water content to completely desiccated lichen thalli takes 2.5 minutes mm^{-2} for thalli from Hochtor, but 15 minutes mm^{-2} for Almeria thalli. This conclusion is supported by the chlorophyll florescence results, which show a much slower rate of decrease in activity in Almeria thalli (Fig. 2).

Samples from the dry site Almeria show both improved water uptake and reduced water loss. A reduction of water loss in lichens seems remarkable, because lichens, as poikilohydric organisms are known for their passive water control and unregulated loss of water over the whole thallus surface. Nevertheless, Beckett (1995) showed that lichens from dry habitats seem to make better use of their water, by maintaining turgor down to low relative water contents. The reduced rates of water loss found here, may be the result of increased diffusive resistance caused by the thicker epinecral layer. This layer is often described as amorphous, and is composed of decomposing hyphae with indistinct cell lumina; it forms a very dense layer that can act as a barrier to water loss, more so than the upper cortex. In the revised generic concept of Parmelioid lichens (Crespo et al. 2010) a pored epicortex is an important diagnostic feature beside molecular, morphological and chemical evidence. The epicortex proabably provides an extra layer of protection against evaporation. A thick epinecral layer, as present in the samples from the dry site Almeria may therefore account for such a reduction in water loss. Nevertheless, developing a thick epinecral layer also seems contradictory to improved water gain, because it is also reported to have hydrophobic properties (Lakatos *et al.* 2006). The occurrence of hydrophobins, proteins unique to mycelial fungi, has been suggested to be important for the survival of lichens (Wessels 2000). According to Honegger (1991), a hydrophobic lining of gas spaces allows efficient apoplastic transport of water and solutes between the symbionts, and permits optimal gas exchange during wet periods. Therefore, very low water repellency of the samples from site Almeria is unsurprising. The suggested explanation for this result derives from the structure of the

epinecral layer itself and how this influences the lichen surface (Fig. 1C and D). In dried thalli, the epinecral layer has open cracks (Fig. 1E), thus increasing the surface area and facilitating water uptake by cohesion and adhesion, leading liquid water towards the photobiont layer (Fig. 1E and F). With $WHC_{shaking}$ being close to 50 mg H_2O cm^{-2} (Table 2, 10 mg H_2O cm^{-2} equates to 0.1 mm dew or rain) these lichens use the rare rain evens more often than dewfall (Gauslaa et al. 2014). Both findings support the explanation that a functional role of the epinecral layer is to influence the lichen hydrology. To our knowledge, this has not been previously described. The function of the epinecral layer is usually suggested to be protection against high light stress (Büdel & Lange 1994, Büdel *et al.* 1997, Rikkinen 1995, Kappen *et al*. 1998, Dietz *et al*. 2000). For chlorolichens, drying combined with light exposure can be particularly harmful (Gauslaa *et al*. 2012) and it was suggested that the ability to recover, correlates positively with increasing species-specific water holding capacities (WHC). In Almeria, light intensities and UV-radiation are much higher throughout the year (Table 1), and in this population the thicker epinecral layer is therefore necessary to prevent light damage. In the Hochtor site, where light intensity is less and exposure time to both PAR and UV are shortened due to snow cover, such protection would not be required or beneficial to the lichen.

In the wet site of Hochtor, the lichens experience a different set of stresses. Water saturation for many hours a day may result in negative carbon gain for two reasons. First high respiration rates during the night and under the snow cover can influence carbon balance negatively, and second CO_2 diffusion resistance is high in water supra-saturated thalli, thus reducing the substrate for photosynthesis (Cowan *et al.* 1992). The high $WHC_{shaking}$ values indicate that these lichens are more often exposed to rain events of about 40 mm precipitation (Gauslaa et al. 2014), which underlines their frequent water saturation. For lichens, it is essential to minimize periods of water supra-saturation. Indeed, the functional aspects that we report here for the lichens from the wet site Hochtor are fast desiccation times, high hydrophobicity, low maximum water uptake relative to the thallus specific dry weight and a broad range of thallus water contents for optimal photosynthesis. All of these may be explained by specific thallus anatomy, which includes a very thick medulla layer and is best quantified by the high STM values (Table 2). The medulla is the fungal zone in the lichen thallus, composed of hyphae, with cell walls often incrusted with crystalline secondary metabolites. It was shown that lichen substances

did not maintain the water-free diffusion pathways (Lange *et al*. 1997) and the authors suggested that these pathways are rather maintained by structural changes. Together with numerous hydrophobic air spaces in the medulla, supra-saturation with water is minimized or even avoided (Lange *et al.* 1993). The morpho-anatomical adjustments leading to water repellency of the upper layers involve reduced STA for the samples from site Hochtor. The parameter of STA is analogous to specific leaf area (SLA), in higher plants, which can yield information about life strategies. Species with low SLA conserve acquired resources, due to their large dry matter content, high concentration of cell walls and secondary metabolites, and high leaf and root longevity (Marron *et al.* 2003). By applying these features to lichens, the lower the STA, the lower the fitness and the more lichen material is needed to support the same surface area. Our results show higher STA values for lichens from the dry site Almeria, which means that these lichens have a higher fitness. One conclusion from this result might be that anatomical and functional adjustments within *P. decipiens* are more easily made towards dryness and high light stresses than towards water supra-saturation, a common phenomenon in the wet site Hochtor. This conclusion may be of general interest towards regions with climate change predictions that include increased flood and heavy rain risks (IPCC 2012), as the conditions are expected to occur in the future in many areas that sustain natural BSCs covers. Accumulations of such events may influence the natural BSC more severely than increasing drought.

This study suggests that two populations show variations in morpho-anatomical traits that result from their native environments climatic differences. These differences could result from ecotypic variation or phenotypic plasticity. Increasingly, recent studies on plant plasticity describe not only growth rates documentation and morphological parameters, but also functional aspects of plasticity. The plasticity of functional traits (both long- and short term) can contribute to the ability of species to occupy diverse and variable habitats in nature (Sultan *et al.* 1998). Phenotypic plasticity plays an important role in community ecology because it contributes to the ability of species to withstand environmental changes, such as those caused by human disturbance. The timescale of such changes is often too short for an evolutionary response, thus species that lack sufficient plasticity might be at risk of altered reproduction, degradation or extinction (Sultan 2000). On the other hand, ecotypic variation would result in the two populations also being different on a genetic level. This would suggest that the

observed differences are not due to the species plasticity and could therefore be at risk to climate change and habitat loss. This study has focused on purely morphological and physiological characteristics of the lichen *P. decipiens.* In order to reveal a complete picture of the variation of this important soil crust lichen molecular analysis has to be included. The next step is to investigate the genetic diversity and acclimation potential of both the algal and fungal partners of *P. decipiens* from the two populations at the climatically distinct sites.

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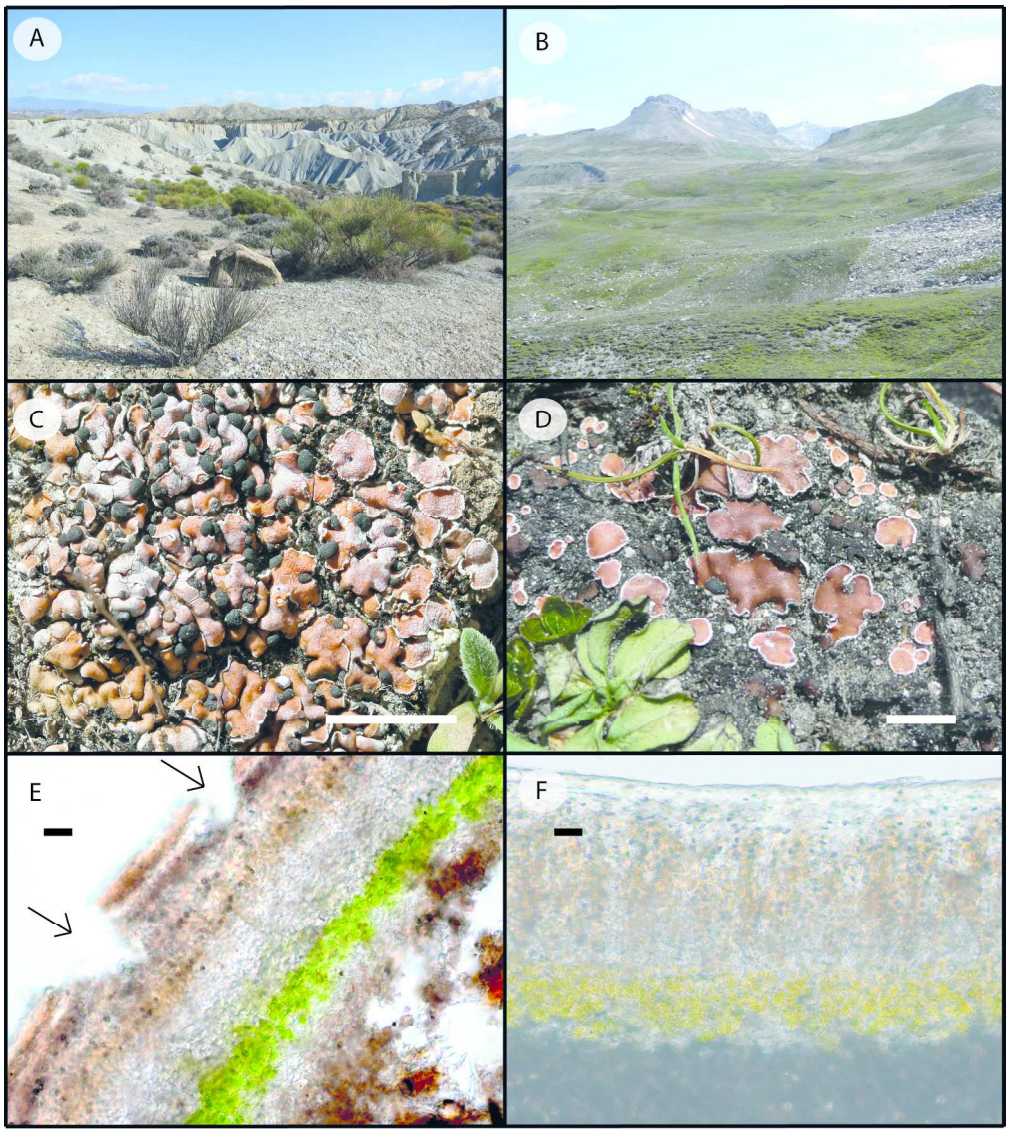
Figure captions:

Figure 1: Characteristics of *Psora decipiens.* A) Study site Almeria overview, B) study site Hochtor overview; C) natural appearance at study site Almeria (photo: Martin Westberg); D) natural appearance at the study site Hochtor; E) cross section from site Almeria with the thick cracked (arrows) epinecral layer; F) cross section from site Hochtor with a continuous epinecral layer and a thick medulla including a thick photobiont layer. White scale bars indicate 1 cm, black bars indicate 20µm.

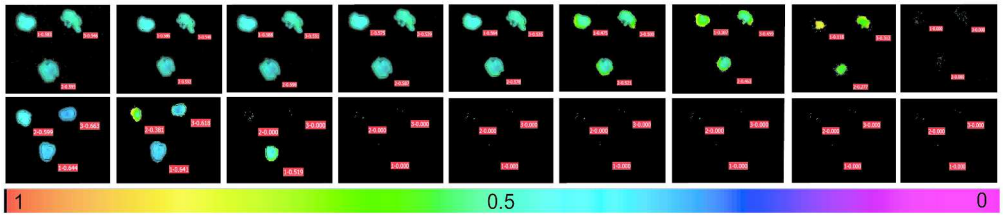
Figure 2: Dehydration kinetics of *Psora decipiens*. False color chlorophyll fluorescence images of the effective quantum yield (Y) of photosystem II distribution over three thalli from site Almeria (upper

row) and site Hochtor (lower row), obtained using an Imaging PAM (Walz GmbH, Effeltrich, Germany). Yield intensity is color coded covering a range from 1-0 with red indicating very high values and violet low values. Red flags indicate exact Yield values at a chosen area of interest in the picture. Pictures where taken every 2 minutes.



Characteristics of Psora decipiens. A) Study site Almeria overview, B) study site Hochtor overview; C) natural appearance at study site Almeria (photo: Martin Westberg); D) natural appearance at the study site Hochtor; E) cross section from site Almeria with the thick cracked (arrows) epinecral layer; F) cross section from site Hochtor with a continuous epinecral layer and a thick medulla including a thick photobiont layer. White scale bars indicate 1 cm, black bars indicate 20µm.

188x211mm (300 x 300 DPI)



Dehydration kinetics of Psora decipiens. False color chlorophyll fluorescence images of the effective quantum yield (Y) of photosystem II distribution over three thalli from site Almeria (upper row) and site Hochtor (lower row), obtained using an Imaging PAM (Walz GmbH, Effeltrich, Germany). Yield intensity is color coded covering a range from 1-0 with red indicating very high values and violet low values. Red flags indicate exact Yield values at a chosen area of interest in the picture. Pictures where taken every 2 minutes.

297x67mm (300 x 300 DPI)

Table 1: Climate data at the study sites. Climate data are differentiated by summer and winter for both investigation sites. Summer: April-September, Winter: October-March, Almeria: April 2012-March 2014, Hochtor: August 2012-July 2014. Shown are mean values with standard deviation where appropriate, maximum and minimum values recorded across the measuring period, average rainfall per season and snow cover duration. PAR and UV are based on daily average and maximum values. a: values are significantly different within the sites (summer vs. winter), b: values are significantly different between sites (eg. Site Almeria summer vs. site Hochtor summer).

		Site Almeria		Site Hochtor	
Parameter		Summer	Winter	Summer	Winter
Air temp. (°C)	Average	23.0 ± 6.6^{ab}	13.6 ± 5.8^{ab}	2.0 ± 4.6^{ab}	-3.7 ± 3.0^{ab}
	Max	43.8	34.8	19.86	14.6
	Min	2.8	0.0	-7.5	-18.6
Humidity. (%)	Average	51.4 ± 20.5^{b}	60.6 ± 19.7^{b}	92.4 ± 12.3^{b}	93.1 ± 9.5^{b}
PAR (µmol m^{-2} s^{-1})	Average	962.5^{ab}	619.8^{ab}	441.8^{ab}	152.8^{ab}
	Max	2650	2406	2680	1862
UV_{A+B} (µmol m^{-2} s^{-1})	Average	89.69^{ab}	60.6^{ab}	77.8^{ab}	33.8^{ab}
	Max	346.9	266.8	384.2	244.6
Rain (mm)	Average	25.5^{ab}	91.8^{ab}	558.3^{ab}	75.45^{ab}
Snow cover	Year	None	None	3 months	6 months

Table 2: Comparison of anatomical and hydrological characteristics of lichen thalli deriving from the wet exposed site Hochtor and the dry site Almeria. Shown are mean values with standard deviation and significance levels from t-tests.

Thallus morphology			Significance of difference between dry and wet exposed thalli		
parameter	Site Almeria	Site Hochtor	t	df	p
Epinecral layer thickness (µm)	92.2 ± 18.8	70.1 ± 9.8	7.3	98	0.000
Photobiont layer thickness (µm)	91.5 ± 16.2	93.0 ± 20.2	-0.7	398	0.4
Medulla thickness (µm)	102.4 ± 38.6	224.6 ± 59.4	-24.4	398	0.000
Photobiont/ Medulla ratio	0.89	0.41			
Specific thallus area (mm^{-2} mg)	4.7 ± 0.9	2.9 ± 0.3	5.6	19	0.005
Specific thallus mass (mg cm^{-2})	22.3 ± 3.8	36.7 ±7.6	5.6	19	0.005
Thallus hydrology					
Maximum water uptake relative to the thallus specific dry weight (mg H_2O/mg dry weight)	2.1 ± 0.7	1.4 ± 0.1	-4.1	34	0.000
WC opt (%)	109.7 -156.1	131.8 – 195.4		2	0.03
WHC (mg H_20 cm^{-2})	46.4 ± 12.8	51.6 ± 9.9	-2.5	19	0.1
WDPT (sec)	1.2 ± 0.3	168.4 ± 15.8	-4.1	28	0.000
Drying rate (min μl^{-1} mm^{-2})	34.1 ± 28.8	5.3 ± 4.3	-4.2	34	0.000